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OSTEOLOGY AND RELATIONSHIPS OF SOUTH AMERICAN CHARACID FISHES OF SUBFAMILIES LEBIASININAE AND ERYTHRININAE WITH SPECIAL REFERENCE TO SUBTRIBE NANNOSTOMINA

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OSTEOLOGY AND RELATIONSHIPS OF SOUTH AMERICAN CHARACID FISHES OF SUBFAMILIES LEBIASININAE AND ERYTHRININAE WITH SPECIAL REFERENCE TO SUBTRIBE NANNOSTOMINA[1]

By Stanley H. Weitzman

Introduction

The present work is the result of an attempt to determine the relationships of two characid genera, *Nannostomus* and *Poecilobrycon*, to other members of the cypriniform family Characidae. The two genera include about eight known species of small characids found in forest brooks of South America. These species are here assigned to the subtribe Nannostomina. Although the first known species of this group was described in 1872, adequate investigation of morphological evidence for their relationships has never been undertaken. Previous investigations have been superficial in scope and often inaccurate in fact primarily because of the small size of these fishes. The total cranial length is usually 5–10 mm. and the largest recorded specimen is 44.5 mm. in standard length. In some cases, despite the lack of adequate morphological data, certain ichthyologists have

[1] This paper is the second of three parts based on a dissertation submitted to the Department of Biological Sciences, Stanford University, California, in partial fulfillment for the degree of Doctor of Philosophy. See Weitzman (1962) for the first part.

shown rather good intuitition in their interpretation of the relationships of these fishes; however, others have not been so fortunate in their interpretation and these fishes have been shifted about in the classification of characids until it is very difficult to obtain from the literature a concept of their affinities.

Investigation of *Nannostomus*, *Poecilobrycon*, and their relatives led to comparison of two widely divergent characid subfamilies, the Characinae, treated by Weitzman (1962), and the Lebiasininae, treated here. In addition the Erythrininae, another divergent subfamily of the Characidae, are compared with the Lebiasininae because these two groups of characids often have been thought to belong to a single group. Although the work began as an effort to determine the relationships of *Nannostomus* and *Poecilobrycon*, its most important result concerns the relationships of the subfamilies Lebiasininae and Erythrininae.

The morphological data obtained in the present study has resulted in the following classification, the names given below being used throughout this paper (see pages 148 to 152 for a full treatment of the classification):

Subfamily Lebiasininae
  Tribe Lebiasinini
  Tribe Pyrrhulinini
    Subtribe Pyrrhulinina
    Subtribe Nannostomina
Subfamily Erythrininae

For the loan of specimens, I am indebted to Dr. George S. Myers of Stanford University, Mr. W. I. Follett of the California Academy of Sciences, Dr. James Böhlke of the Academy of Natural Sciences of Philadelphia, and Mr. Loren P. Woods of the Chicago Natural History Museum. I am indebted especially to Dr. George S. Myers for critically reading much of the manuscript and offering aid and advice during most of its preparation. In addition, the following persons have read the manuscript at various stages, all providing very useful help: Mrs. Lillian Dempster of the California Academy of Sciences, Drs. Myra Keen and Warren Freihofer of Stanford University, and Drs. Leonard P. Schultz, Robert H. Gibbs, Jr., and Victor G. Springer of the U.S. National Museum.

The work was done at the Department of Biological Sciences, Division of Systematic Biology of Stanford University, at the Department of Anatomy, Stanford University School of Medicine, and at the U.S. National Museum, Smithsonian Institution.

Material Examined

This study is based on the examination of the skeletal preparations listed below. All specimens are alizarin preparations unless otherwise noted. In addition, considerable reference has been made to osteological preparations listed in Weitzman (1962, pp. 11–17). The methods of preparing specimens for osteological investigation are the same as those I used earlier (Weitzman, 1954; 1962).

The osteological drawings of *Poecilobrycon harrisoni* Eigenmann are based on one specimen (Stanford University 50245), 36.4 mm. in standard length. This specimen, together with eleven others, was found in the collections of the Division of Systematic Biology of Stanford University. These specimens had no data other than "British Guiana, Georgetown." Six additional aquarium-reared specimens (Stanford University 50244), 9.5 to 21.0 mm. in standard length, were stained with alizarin and compared with the specimen used for drawing. Since general proportions and shapes in the osteological drawings were delineated by optical methods, some distortion can be found in the figures. This is especially noticeable in figures 2–6, wherein the anterior cranial and snout region is somewhat foreshortened. All illustrations are by the author.

In the list below, CAS refers to the California Academy of Sciences; CAS(IUM) refers to specimens belonging to the California Academy of Sciences but previously deposited at Indiana University and still bearing an Indiana University number; SU refers to specimens belonging to the Division of Systematic Biology, Department of Biological Sciences, Stanford University; USNM refers to the United States National Museum; ANSP refers to the Academy of Natural Sciences of Philadelphia.

Copeina guttata (Steindachner): SU 51692, two (of four), SL 56.5–57.0 mm., Peru, creek near Yurimaguas, November 1920, W. R. Allen.

Copella nattereri (Steindachner): CAS 20743, four (of 35), SL 23.5–35.5 mm., Brazil, State of Pará, Lagôa Grande [probably Lagôa Grande do Javari about 35 mi. northwest of Santarém] July 17, 1924, Carl Ternetz.

Erythrinus erythrinus (Bloch and Schneider): SU 57678, four, SL 52.0–99.5 mm., Peru, creek near Yurimaguas, November 1920, W. R. Allen.

Hoplerythrinus unitaeniatus (Agassiz): CAS(IUM) 17106, one (of four), SL 97.0 mm. Bolivia, Cuchuela [Cachuela] Esperanza, March 1922, N. E. Pearson; USNM 163188, one (of four), SL 86.9 mm., Venezuela, a few miles off Puerto Ayacucho, "Amazon territory," March 13, 1950, J. A. Rivero.

Hoplias malabaricus Bloch: CAS(IUM) 17107, five, SL 31.0–108.0 mm., Bolivia, Huachi, at junction of the Río Bopi and Río Cochabamba [Santa Elena], Río Beni basin, September–October 1921, N. E. Pearson; SU 3106, one, dry skeleton, cranium 31 mm. in total length, Brazil, Marajó Island, Río Tocantins, C. F. Hart.

Lebiasina bimaculata Valenciennes: CAS(IUM) 15171, three (of 30), SL 57.5–60.9 mm., Peru, Piura, January 11, 1919, Carl H. Eigenmann.

Nannostomus beckfordi Günther: SU 50258, six (of 44), SL 22.0–26.5 mm., originally from SU 50257, Brazil, State of Pará, south bank of Río Amazonas, "Río Urara," June 26, 1924, Carl Ternetz.

Nannostomus digrammus Fowler: SU 50249, two, SL 16.3–19.4 mm., Brazil, State of Amazonas, Manaos [Manaus], 1865, Louis Agassiz; SU 50251, three, SL 18.0–22.8 mm., Brazil, State of Amazonas, Igarapé do Mãi Joana, a tributary of the Rio Negro near Manaos [Manaus], December 25, 1924, Carl Ternetz.

Nannostomus espei (Meinken): ANSP 73873, one, SL?, British Guiana, an unnamed creek, tributary to the Paruma River, itself tributary to the Mazaruni River via the Kamarang River, Pakaraima Mountain region of western British Guiana, 1955, Louis Chung; SU 50252, one, SL 25.0 mm., aquarium specimen, locality data unknown but probably the same as ANSP 73873.

Nannostomus marginatus Eigenmann: SU 54119, three (of 32), SL 19.0–21.5 mm., originally from SU 50219, Brazil, State of Pará, Lagôa Grande [probably Lagôa Grande do Javari about 34 mi. northwest of Santarém], August 20, 1929, Carl Ternetz.

Nannostomus trifasciatus Steindachner: SU 50223, one, SL 29.5 mm., British Guiana, no other data; SU 54130, one (of two), SL 31.5 mm., aquarium specimen, "from the Amazon," sent to G. S. Myers by Frederick Stoye.

Piabucina festae Boulenger: SU 51068, four (of 12), SL 60.5–71.5 mm., Colombia, Río Truandó, a western tributary of the Río Atrato near Río Sucio, 1913, C. E. Wilson; USNM 167795, one (of six), SL 70.0 mm., same data as preceding.

Piabucina panamensis Gill: USNM 109234, two (of seven), SL 77.7–84.0 mm., Panama, Cativá, March 2, 1937, S. F. Hildebrand.

Piabucina erythrinoides Valenciennes: USNM 121400, three (of 27), SL 35.1–101 mm., Río Chama at Estanques, State of Mérida, Venezuela, April 3, 1942, L. P. Schultz.

Piabucina species?: USNM 123796, two (of six), SL 64.1–67.3 mm., Colombia, Río Magdalena, Cecil Miles.

Poecilobrycon eques (Steindachner): SU 50247, two (of five), SL 28.5–30.0 mm., originally from SU 50229, Brazil, State of Amazonas, São Gabriel [Uaupés], Río Negro, rockpools below rapids, February 1, 1925, Carl Ternetz; SU 50224, three, SL 25.8–32.5 mm., aquarium specimens, no other data.

Poecilobrycon harrisoni Eigenmann: SU 50246, one, SL 29.5 mm., originally from SU 50245, British Guiana, Georgetown, collector unknown; SU 50245, one (10 unstained), SL 36.4 mm., British Guiana, Georgetown; SU 50244, six, SL 9.5–21.0 mm., aquarium specimens, reared by S. Weitzman.

Poecilobrycon unifasciatus (Steindachner): CAS(IUM) 11704, one (of 10), SL 33.0 mm., British Guiana, Rockstone sandbank, Essequibo River, 1908, C. H. Eigenmann; SU 50268, two, SL 27.8–30.4 mm., aquarium specimens, no other data.

Pyrrhulina filamentosa Valenciennes: CAS(IUM) 12186, four, SL 14.7–20.2 mm., British Guiana, Aruka River, 1908, C. H. Eigenmann.

Pyrrhulina semifasciata Steindachner: CAS(IUM) 12172, one, SL 58.1 mm., British Guiana, Holmia Creek, 1908, C. H. Eigenmann.

Pyrrhulina spilota Weitzman: USNM 197523, two (of 19), SL 41.5–50.4 mm., first generation descendants of holotype and paratype.

Pyrrhulina vittata Regan: USNM 197524, SL 26.0 mm., aquarium specimen, locality unknown.

Historical Review of the Classification of *Nannostomus* and *Poecilobrycon*

Günther (1872, p. 146) described the first member of the Nannostomina, *Nannostomus beckfordi*. Of its relationships with other characids, he simply stated: ". . . allied to *Lebiasina*, but with a totally different form of the snout and mouth." He considered it to belong to his first group of characids, the Erythrina (Günther 1864, pp. 278 and 281), which included the genera *Hoplias*, *Erythrinus*, *Lebiasina*, *Pyrrhulina*, and *Corynopoma*. They were defined as those characids without an adipose fin.

Steindachner (1876, p. 130) thought *Nannostomus* should be placed in or near the group Anostomatina [2] of Günther (1864, pp. 279, 303). Günther's Anostomatina included the genera *Anostomus*, *Rhytiodus*, and *Leporinus*. Steindachner (1876, p. 122) pointed out that the presence or absence of the adipose fin in *Nannostomus* (=*Nannostomus* plus *Poecilobrycon* of later authors) is not of importance in determining their relationships with other characids because this fin may be present or absent in specimens of *Poecilobrycon eques*.

Eigenmann and Eigenmann (1891, p. 49) placed *Nannostomus* in their subfamily Anostomatinae, which also included *Anostomus*, *Laemolyta*, *Characidium*, *Rhytiodus*, *Leporellus*, and *Leporinus*. Boulenger (1904, p. 576), following Steindachner's and Eigenmann's precedent, placed the genus *Nannostomus* in the subfamily Anostominae.

Eigenmann (1909b, p. 35–36) placed the genera *Nannostomus*, *Poecilobrycon*, and *Archicheir* (the latter two therein described) in his undefined subfamily Nannostomatinae; however, the name Nannostomatinae first appeared in Eigenmann (1909a). He also included the genera *Characidium* and *Microcharax* in this subfamily. Eigenmann (1910, p. 427) again listed his subfamily Nannostomatinae and, in addition, included the genus *Jobertina*. Eigenmann may have held the opinion that the members of his subfamily Pyrrhulininae are allied to *Nannostomus* and *Poecilobrycon* for he placed them immediately after his Nannostomatinae. These two subfamilies were separated widely from his Erythrininae. Eigenmann's Anostomatinae (including *Leporinus* and relatives) immediately preceded his Nannostomatinae. Apparently at that time he thought them related. Eigenmann (1912, p. 254), in a key to the subfamilies of characids from British Guiana, first defined the subfamily Nan-

[2] According to Miller (1897, p. 132), family group names formed from adjectives used substantively, e.g., *Nannostomus* and *Anostomus*, should not be terminated by "-atidae" or "-atinae." Accordingly, Günther's *Anostomus* should become Anostomina, not Anostomatina, or Anostominae, not Anostomatinae.

nostomatinae. There are three important errors in Eigenmann's concept of this subfamily's morphology. Teeth are present in the maxillary, not absent; the gill membranes are joined to each other but free from the isthmus, not slightly united; and the parietal fontanel is absent, not present as Eigenmann indicated.

Regan (1911, p. 21) placed the genera *Nannostomus* and *Characidium* in the Nannostominae and included this subfamily in his family Hemiodontidae. This family consisted only of his Hemidontinae and Nannostominae.

Cockerell (1914, p. 98–99), in a study of characid scales, noted the close resemblance of the scales of *Nannostomus* and *Pyrrhulina* and, on this basis alone, found reason to more closely associate *Pyrrhulina* with *Nannostomus* than *Poecilobrycon* with *Nannostomus*. He also noted the very different structure of the scales of *Characidium*. I find that the scales of *Poecilobrycon* and *Nannostomus* are much alike and, in addition, are very similar to those of *Pyrrhulina*, *Copella*, and *Copeina*. In confirmation of part of Cockerell's work, however, the osteology and scales of *Characidium* differ quite widely from the osteology and scales of any of the other genera discussed here.

Gregory and Conrad (1938, pp. 324, 344–347) followed Regan (1911) in relating *Nannostomus* and *Poecilobrycon* to *Hemiodus* and its relatives. They placed *Nannostomus* and *Poecilobrycon* in a subfamily (Hemiodontinae) considered by them to be widely separated from the subfamily (Characinae) containing *Pyrrhulina*. As shown below, my work indicates that *Nannostomus*, *Poecilobrycon*, and *Pyrrhulina* are related rather closely and are placed in the tribe Pyrrhulinini.

Fowler (1950, pp. 253–263) considered the genera *Characidium*, *Microcharax*, *Nannostomus*, *Archicheir*, and *Poecilobrycon* as constituting the subfamily Nannostominae (apparently following Eigenmann, he spelled it Nannostomatinae). He placed this subfamily nearest his subfamilies Leporininae and Parodontinae but did not comment on relationships or define his groups.

Hoedeman (1950a, p. 14) established the tribe Nannostomini to include the genera *Nannostomus*, *Poecilobrycon*, and his newly proposed *Nannobrycon*. He apparently did not consider that the genus *Archicheir* belonged to his Nannostomini, for he excluded it from his treatment.

In his first paper on *Nannostomus* and relatives, Hoedeman (1950a, p. 11) considered his Nannostomini to be related to the Hemiodontinae; however, he excluded *Characidium* from relationship with the Hemiodontinae. He presented no evidence for this opinion. Hoedeman (1954a, p. 83) reconsidered his classification and placed the tribe (emended to Nannostomidi) in his family Erythrinidae, a family he

then considered as comprising two subfamilies, Erythrininae and Anostominae. He here excluded the Hemiodontinae from his Erythrinidae. His subfamily Erythrininae comprised four tribes, Lebiasinidi, Erythrinidi, Pyrrhulinidi, and Nannostomidi. He did not present evidence for this classification but he did remark (words in brackets are mine): "*Poecilobrycon* cannot be derived from either of these genera [i.e., *Nannostomus* or *Nannobrycon*], nor vice versa. The two groups probably had a common ancestor, close to the present day *Pyrrhulina*, to which both are more closely related than to each other." Hoedeman, however, placed *Poecilobrycon*, *Nannostomus*, and *Nannobrycon* in one group and the *Pyrrhulina* in another. As will be shown below, it is my opinion that the members of the Nannostomina as defined below are more closely related to each other than to any other characids, but that Hoedeman was correct at that time in suspecting their relationship to be with *Pyrrhulina*. Hoedeman (1954b, pp. 68–84, and 1956b, pp. 547–551), however, once again reconsidered his classification of *Nannostomus* and *Poecilobrycon* and placed them with *Hemiodus* and relatives, excluding them from close realtionship with *Pyrrhulina*.

In summary, the Nannostomina have been thought to be related to *Lebiasina* and its relatives, *Erythrinus* and its relatives, *Pyrrhulina* and its relatives, *Characidium*, and finally to *Hemiodus* and its relatives. As will be shown, their morphological relationships are with *Pyrrhulina*, *Lebiasina*, and close relatives. Inadequate morphological investigations have been the primary cause of this divergence of opinion.

Historical Review of the Classification of the Erythrininae and Lebiasininae

Since in the present work *Nannostomus* and *Poecilobrycon* have been found to belong to the subfamily Lebiasininae, a historical review of their relationships to other characids would not be complete without a historical review of the Lebiasininae. Because the Lebiasininae and Erythrininae have been associated closely by many authors, both are reviewed.

Valenciennes, in Cuvier and Valenciennes (1846, p. 480), established the "famille des Erythroides" for the reception of the genera *Macrodon* (=*Hoplias*), *Erythrinus*, *Lebiasina*, and *Pyrrhulina*. He defined these fishes as having a double swim bladder that is sometimes cellular, teeth on their jaws and palate, the cheek covered by a large subopercle, the belly always rounded, and no pyloric caeca. Apparently, Valenciennes interpreted the small autogenous "supraopercular" element of *Hoplias* as the opercle and the large true opercle as the subopercle.

Günther (1864, pp. 278, 281–288) added the genus *Corynopoma* to Valenciennes' family grouping. This genus originally was considered by Gill (1958, pp. 422–428) to have affinities with the Characinae. Regan (1906, p. 382; 1911, p. 16) has shown good reasons for not placing *Corynopoma* with the genera *Hoplias*, *Erythrinus*, and *Hoplerythrinus*.

Gill (1858, pp. 410–413) established the family Erythrinidae for *Pyrrhulina*, *Erythrinus*, and *Lebiasina*. Eigenmann and Eigenmann (1889, pp. 100–115) followed Günther (1864) in including *Corynopoma* in what otherwise essentially equals Gill's family Erythrinidae. Neither Günther nor Eigenmann and Eigenmann had seen examples of Gill's *Corynopoma*. The Eigenmanns, however, chose to give the group subfamily rank (Erythrininae) within the Characidae. The Eigenmanns listed characters for the Erythrininae as follows:

> Adipose fin none. Gill opening wide, the membranes slightly united, free from the isthmus. Nares approximated. Teeth well developed, at least in the jaws; pharyngeal teeth villiform. Cheeks covered by the suborbital bones. Brain case entirely closed above. Body elongate, slender, fusiform or subfusiform. Back not greatly arched, belly rounded. Dorsal short, of 8 to 15 rays. Intestine short. Carnivorous.

This definition does not exclude all members of the Characinae or members of some of the other subfamilies of characids.

Regan (1911) included all the members of Gill's Erythrinidae in his Characidae; however, he separated *Pyrrhulina* widely from *Lebiasina* and *Piabucina* because he found that *Pyrrhulina* lacked ectopterygoid teeth while *Lebiasina* and *Piabucina* possessed them. Examination of many characids indicates that the presence or absence of ectopterygoid teeth is of minor importance because, in some species that normally possess them, they may be unilaterally or bilaterally absent in a few specimens. They may also be present in one species but absent in otherwise closely related species, e.g., *Charax* and its relatives.[3]

Regan (1911) maintained *Erythrinus*, *Hoplerythrinus*, and *Hoplias* in the subfamily Erythrininae and the genera *Lebiasina* and *Piabucina* in the subfamily Lebiasininae. He placed *Nannostomus* and *Poecilobrycon* in his Hemiodontidae because their premaxillaries are movable, because he thought they had no ectopterygoid teeth, and because he misinterpreted the palatine arch.

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[3] The establishment of the family Acestrorhynchidae by Fernandez-Yepez (1955, p. 450) and the genus *Charaxodon* by Fernandez-Yepez (1947, p. 1), based principally, if not wholly, on the presence or absence of ectopterygoid teeth (= the teeth of the "palatine" of Fernandez-Yepez) should be reviewed with a more critical approach. Böhlke (1958, p. 70) considered *Charaxodon* to be a synonym of *Morallesia*.

Regan (1912) lumped the genera *Chalceus*, *Pyrrhulina*, *Copeina*, and *Pogonocharax* into a "natural group," stating that they differed from the rest of the Characidae by a very large mesethmoid (= ethmoid of this work), oblong or elongate body form, rounded abdomen, flattish upper surface of the head, large scales, and short dorsal and anal fins. These are superficial characters and do not indicate true relationships. The osteology of *Chalceus* appears to be in many respects like that of *Brycon* and there is reason to believe that *Chalceus* may have been derived from *Brycon* or a very close ancestor. In any event, its osteology is typically that of the Characinae as defined by Weitzman (1962). The case of *Pogonocharax rehi*, a fish described by Regan and presumed by him to be from South America, was reviewed by Myers (1956b, p. 13); the fish is not a characid but an Asiatic cyprinid of the genus *Esomus*.

Gregory and Conrad (1938, pp. 324, 343–344) recognized the subfamily Erythrininae for the inclusion of the Erythrininae and Lebiasininae of Regan (1911). Superficially, Regan's two subfamilies do look much alike but they are separated by the characters listed below in the classification. Gregory and Conrad (1938, p. 343) have noted the resemblance of *Hepsetus* (= *Sarcodaces*) to *Hoplias;* indeed, *Hepsetus* possesses a supraopercular like *Hoplias*. The cranial bones do have a superficial and perhaps even a phylogenetically significant resemblance to those of *Hoplias*. Basically, however, the osteology of *Hepsetus* is more like that of the Characinae, especially with regard to the pectoral girdle. In addition, *Hepsetus* has four branchiostegal rays, a clear anastomosis between the dermopterotic and supraorbital laterosensory canals, no accessory ectopterygoid, and the usual characid number of eight orbital bones. Certain features of the skull, however, such as the frontal-sphenotic articulation and the presence of a supraopercular are characters in common with the Erythrininae but not the Characininae and suggest that the relationships of *Hepsetus* should be investigated further. In addition, the possible relationships of *Ctenolucius* and *Boulengerella* with *Hepsetus* should not be neglected. Preliminary examination indicates that the relationships of *Acestrorhynchus* and *Acestrorhamphus* are probably with *Charax*, *Roeboides*, and other closely related genera in the Characinae, not with *Boulengerella* and *Ctenolucius* as assumed by Gregory and Conrad (1938, pp. 323–324, 338–344). These authors followed Regan (1911) in placing *Nannostomus* and *Poecilobrycon* with members of the Hemiodontinae.

Hoedeman (1954b, p. 55; 1956a, p. 12) presented a classification of the major characid groups. Most of his work appears to be speculation. The only morphological data of any value was a superficial comparison of scales from several characids. In his 1956 classification, Hoedeman

separated characids into three families, one of which was the Erythrinidae. He divided this family into two subfamilies. The first, the Erythrininae, contains his Lebiasinidi (= Lebiasinini of the present work), Erythrinidi (= Erythrininae), Pyrrhulinidi (= Pyrrhulinina) and Nannostomidi (= Nannostomina). The second subfamily of Hoedeman's Erythrinidae is the Anostominae. In this group he placed four tribes, Curimatidi, Anostomidi, Hemiodontidi, and Prochilodidi. Hoedeman (1956a, p. 12) stated:

> Vers le milieu de l'eocene, les Erythrinidae se divisent en deux sous-familles: (a) Erythrininae, avec les tribus actuelles: (1) Lebiasinidi, (2) Erythrinidi, (3) Pyrrhulinidi, et (4) Nannostomidi; et la seconde sous-familles: (b) Anostominae, avec les tribus: (5) Curimatidi, (6) Anostomidi, (7) Hemiodontidi, et (8) Prochilodidi.

There is no fossil evidence for this statement nor is there fossil evidence for any of the other of Hoedeman's phylogenetic and time-sequence inferences and speculations given in his paper.

Piton (1938) described two fossil fishes from the mid-Eocene at Menat, France. Piton thought that these fishes, *Prohydrocyon pellegrini* and *Procharacinus arverniensis*, were fossil characids. Perhaps Hoedeman's use of the date of mid-Eocene is from Piton's paper. It appears now that there is no evidence for characids from the mid-Eocene of France (Weitzman, 1960).

The original evidence presented by Hoedeman (1956a) for his phylogeny was apparently derived from examination of a few representative characid scales. Examination of characid scales of the genera listed in the material section of Weitzman (1962) shows a greater variation in the scale morphology of characid groups than Hoedeman found. Sufficient variation was found among the representatives of the various groups to indicate that, although scales will prove useful as an aid in establishing a classification and for drawing phylogenetic inferences, their use alone, without an attempt to correlate them with many other morphological characters, may more often prove misleading than helpful.

Osteology of *Poecilobrycon harrisoni* and Related Characids

In the osteological discussion below, parts of the skeleton of *Poecilobrycon harrisoni* are described and compared with other species of *Poecilobrycon* and *Nannostomus*. Also, other characid genera and groups thought, either by the present author or other authors, to be pertinent to a discussion of the relationships of the Nannostomina are compared with the basic skeletal plan of *Nannostomus* and *Poecilobrycon*.

Cranium (figs. 2, 3, 4, 5, 6).—The median ethmoid bone is a large, rather thin plate that has a profile in dorsal view as shown in figure 2.

This bone has bilateral posterior lamellae projecting backward under the frontals and contacting the dorsoanterior portion of each lateral ethmoid. The ethmoid probably is mostly of supraethmoidal (dermethmoidal) origin, but an anterior, ventral lamella of the ethmoid that extends inferiorly and posteriorly to contact the prevomer below is probably of endochondral origin. The ethmoidal spine found in most characids (see Weitzman, 1962, figs. 2, 3, 4 of *Brycon meeki*) is reduced to a very small structure. The premaxillaries are not firmly attached (the joint being a loose syndesmosis) and are somewhat movable, being attached to the ethmoid by fairly long, lax ligamentous tissue. They cannot, however, be described as protractile. The cartilagenous part of the ethmoid is restricted to the area between the large prevomer and the ethmoid. A few foramina are present on the dorsoanterior surface of the ethmoid. All species of *Nannostomus* and *Poecilobrycon* have a very similarly shaped ethmoid; however, members of the genus *Nannostomus* have a shorter snout and, therefore, a shorter, more blunt ethmoid than members of the genus *Poecilobrycon*.

The large ethmoid of the genera *Pyrrhulina*, *Copella*, and *Copeina* is very similar to that in the Nannostomina in its relationships to the prevomer, lateral ethmoids, and frontals. It differs, however, in having a broader, more rounded horizontal profile and a very well-developed, though rather obtuse, ethmoidal spine. In the Pyrrhulinina the premaxillaries are attached to the ethmoid by a very slightly movable syndesmotic fibrous joint. The ethmoid of *Lebiasina* and *Piabucina* is generally similar in structure to that of *Pyrrhulina*, *Copella*, and *Copeina*, but proportionately the ethmoidal spine is considerably smaller.

The ethmoids of the Lebiasinini and Pyrrhulinina differ most prominently from those of the Nannostomina in the following manner: The ethmoidal spine is well developed, the premaxillary is firmly fixed to a groove along the anterolateral border of the ethmoid by a tight fibrous joint, and the ethmoid bone is not as oblong or square in horizontal profile, being somewhat more wedge-shaped.

The ethmoid of *Hoplias* (Starks, 1926, p. 160, fig. 8) and *Erythrinus* is quite similar in general form to that of *Brycon* (Weitzman, 1962); however, the joint between the ethmoid and prevomer is bordered by a lateral lamina of cartilage that is in contact with, or approaches, a mass of cartilage on the medial anterior border of the palatine (fig. 4). In the Characinae, only very small amounts of cartilage exist in these areas. The ventral diverging bony ethmoid lamellae, so well developed in the other characid fishes examined, are not at all, or only weakly, developed in the Nannostomina, only weakly so in the Pyrrhulinina and the Lebiasinini, but well developed in the Erythrininae.

The toothless prevomer is concave ventrally and concave dorsolaterally, being an inverted Y-shaped bone in cross section. In small specimens of *Poecilobrycon harrisoni* and in the large adults of some species (*Nannostomus beckfordi* and *N. trifasciatus*), the prevomer is formed of three thin concave plates of bone adhering to, or about, a central cartilaginous core. The two fused dorsal plates contact the ethmoid by a cartilaginous (synchondral) joint and posteriorly by another synchondral joint to the parasphenoid and lateral ethmoid. There is no rhinosphenoid. The posterior shaft of the prevomer, which ordinarily contacts the parasphenoid in the characinae, is extremely short and does not reach the parasphenoid. There are a number of foramina on the ventral surface of the prevomer. Many of these are probably for branches of the ramus buccalis facialis nerve.

Members of the Erythrininae, Lebiasinini, and Pyrrhulinina have a prevomer essentially like that of the Nannostomina; however, the shaft of the vomer is better developed in groups other than the Nannostomina and extends well back onto the parasphenoid. Except for the reduced prevomerine shaft in the Nannostomina, the prevomer of the Lebiasininae is essentially like that of the Characinae.

Each lateral ethmoid projects downward from under its respective frontal and contacts its counterpart at the median vertical plane by a nonmovable synchondral (cartilaginous) joint. The foramen for the olfactory nerve is near the median edge of the lateral ethmoid. An upper medial blade of the lateral ethmoid extends anteriorly and medially to contact a vertical median wall of cartilage behind the prevomer and there forms a nonmovable synchondral joint. Anteroventrally the lateral ethmoid has a process extending forward to contact a sheet of cartilage that extends anteriorly to the lower portion of the prevomer. Ventrally the prevomer is in contact through cartilage with the parasphenoid and posteromedially with the orbitosphenoid. The lateral ethmoid of all members of the Nannostomina and other members of the Lebiasininae is essentially the same. In the Pyrrhulinina and the Lebiasinini the distance between the prevomer and the lower medial portion of the lateral ethmoid is much shorter. That of young specimens of *Hoplias* is similar to that in the Nannostomina, but in older specimens the two bones meet each other. The structural configuration of the lateral ethmoid in the Erythrininae and Characinae is not markedly different in the two groups, and those differences in form that do occur can be correlated with differences in the shape of mouth and snout and their functions.

The frontals of *Poecilobrycon harrisoni* are large, smooth, gently curved bones. They are similar to the frontals of the Characinae in their basic structural relationship to other bones of the cranium; however, the frontal-parietal fontanel is never present in adults and

the epiphyseal bar is relatively small in size. In young specimens a well-developed fontanel is present. A specimen 14.8 mm. in standard length had a well-developed fontanel while a specimen 21.8 mm. in standard length had none. The supraorbital laterosensory canal in the frontal has the normal characid course but with the following exceptions: The portion of the canal that normally is buried in frontal bone over the epiphyseal bar (the mesial or epiphyseal branch) is reduced greatly in length, and the canal that in the Characinae passes backward in the frontal to the pareital (the posterior branch) is absent.

The distribution of major laterosensory canals is the same in the frontal of the Pyrrhulinina as in the Nannostomina although the mesial branch (supraorbital commissure of Branson and Moore, 1962) sometimes is developed better in the Pyrrhulinina. In *Piabucina* the posterior branch is present but it does not reach the parietal. In both *Lebiasina* and *Piabucina* there is a branch of the dermopterotic sensory canal extending backward in the lateralmost edge of the frontal. Posteriorly the dermopterotic canal enters the pterotic. Anteriorly this canal enters the infraorbital canal. In *Hoplias*, *Erythrinus*, and *Hoplerythrinus* the lateral edge of the frontal bone extends outward to contact the spinous process of the sphenotic, completely covering and encircling the dilator groove. This is not true in the Characinae, nor in the Lebiasinini, Pyrrhulinina, or Nannostomina. In these fishes the dilator groove is covered but not encircled by the frontal. Small specimens of *Hoplias* have the frontals and parietals separated by a fontanel, while adults do not. In *Hoplias* and *Erythrinus* the supraorbital sensory canal is the same as in the Nannostomina, but the posterior branch extends into the parietal.

The supraoccipital of *Poecilobrycon harrisoni* is not unlike that of *Brycon* in its position and relationships to other cranial bones. The supraoccipital of the Pyrrhulinina, Lebiasinini, and Erythrininae is quite similar to that of the Nannostomina and differs mainly from the Characinae in the replacement of the supraoccipital spine with a crest.

The exoccipitals, basioccipital, and epiotics of *Poecilobrycon harrisoni* are very much like those of the members of the Characinae and differ in a manner correlated with the widening and flattening of the skull. This may best be seen by comparing the illustration in Weitzman (1962, fig. 5) with figure 5 of the present work. The myodome is much reduced in its vertical depth. The exoccipitals, epiotics, and basioccipital of the Pyrrhulinina, Lebiasinini, and Erythrininae differ from those of the Characinae in having shapes similar to those of the Nannostomina.

The opisthotic is a small tabular bone applied to the joint between the pterotic and exoccipital but lying mostly on the pterotic.

Dorsally the pterotic is overlaid by the parietal and posteriorly contacts the epiotic. Anteriorly and dorsally the pterotic does not reach the frontal but is completely bounded by the sphenotic, while medially it contacts the prootic. Except for lacking a dermopterotic laterosensory canal, for not contacting the frontal, and except for its general shape, the pterotic is much like that of the Characinae. The pterotic of the Pyrrhulinina is like that of the Nannostomina in lacking a laterosensory canal and in not being jointed with the frontal. The Lebiasinini and the Erythrininae have a laterosensory canal in the pterotic and the frontal contacts the sphenotic.

The sphenotics are much like those of the Characinae; their various relationships to other bones have been described under the frontals and parietals. Their relationships to the semicircular canals are the same as in the Characinae.

In their essential relationships to other bones and the soft anatomy, the prootics are not greatly different from those of the Characinae. Detailed comparison of the various foramina of this bone with the foramina of the prootics of the Pyrrhulinini, Lebiasinini, and Erythrininae undoubtedly would prove productive in determining relationships; however, this work must be postponed pending detailed studies of the nerves, veins, and arteries passing through this complicated bone.

The subtemporal fossa is present as a shallow groove along the joint between the prootic and pterotic and is present in all members of the Erythrininae and Lebiasininae.

The pterosphenoid of *Poecilobrycon harrisoni* and other species of the Nannostomina is similar to that in the Characinae, being a large plate in the upper posterior wall of the orbit. The foramen for the trochlear nerve is located at the junction of the articulation between the frontal, pterosphenoid, and orbitosphenoid.

The orbitosphenoid is Y-shaped in cross section; the upper arms of the Y are jointed to the frontals. A foramen for the first cranial nerve is enclosed partially by the orbitosphenoid. Other species in the Nannostomina examined also have an orbitosphenoid that is Y-shaped in cross section. The same is true of the Pyrrhulinina. In the Lebiasinini the cross sectional shape of the orbitosphenoid is more like a V than a Y. In *Hoplias* the foramen for the first cranial nerve is included completely in the orbitosphenoid of adults but included only partially in that of the young. *Erythrinus* has a rather peculiar orbitosphenoid, consisting of a pair of bilateral flat plates attached ventrally by cartilage. In specimens larger than those examined these plates possibly may fuse ventrally, producing a more

"normal" orbitosphenoid. The orbitosphenoid does not have a foramen for the first cranial nerve in the small specimens of the Erythrininae examined, but it may, in larger specimens. An X-ray negative of a specimen of *Hoplias*, 108 mm. in standard length, indicates that a foramen may be included partially in the orbitosphenoid.

Orbital bones (fig. 6).—There are six infraorbital bones in the Lebiasininae and Erythrininae. The supraorbital is absent. The first and second infraorbitals in adult specimens of *Poecilobrycon harrisoni* have a laterosensory tube imbedded within them. The remainder of the infraorbital bones have the infraorbital canal along their ocular edge but it is enveloped only partially in bone. Only *Poecilobrycon eques*, *P. harrisoni*, and *P. unifasciatus* have a sensory tube contained within the bony substance of both the first and second infraorbitals. All other known members of the Nannostomina lack this bony tube in the second infraorbital, the infraorbital canal passing over the surface of the bone. The antorbital is present and well developed in the Nannostomina; it sometimes partially envelops the anterior part of the infraorbital canal. In the Pyrrhulinina the first two infraorbital bones have enclosed canals; sometimes the other infraorbital bones also have enclosed canals in members of this subtribe.

In the Lebiasinini the infraorbital canal may be included within the bony substance of all the orbital bones or it may pass only over the surface of the second through the fifth infraorbital. It may pass either within or over the substance of the antorbital.

In the Erythrininae the orbital bones have an infraorbital canal imbedded in them. There is no supraorbital; the antorbital contains a canal and is fused with the first infraorbital. This is apparently similar to the situation found in certain cyprinodonts and catfishes (see Weitzman, 1962, pp. 28–31). Another possible interpretation is that the antorbital is absent, the first infraorbital having extended into the topographical area of the antorbital.

The elongate nasal bone of the Nannostomina has the usual characid relationship, being a tubular bone connected with, and anterior to, the supraorbital canal of the frontal. In the Pyrrhulinina, Lebiasinini, and the Erythrininae the nasal bone is not greatly different from that of the Nannostomina except for differences correlated with the broader and shorter snouts in these fishes.

Opercular apparatus (figs. 6, 7).—The opercular bones of the Nannostomina differ from those of the Characinae mainly in having a different shape correlated with the elongate and relatively flattened head. The thin interopercle internally covers much of the lower surface of the symplectic, preopercle, metapterygoid, and even some of the quadrate. The preopercle does not extend forward to near the

mandible as it does in the Characinae, Pyrrhulinini, Lebiasinini, and Erythrininae, but it is limited in its anterior extent to an area under the long, slender, lower, posterior process of the quadrate. The opercle and subopercle are similar in Lebiasininae and Erythrininae and are not markedly different from those of the Characinae.

Upper jaw (figs. 6, 7).—The premaxillaries of the Nannostomina bear a single row of one to seven small cuspid teeth. A row of "replacement" teeth is present behind the main outer row. The premaxillary is not divided into upper and lower processes but is more or less lenticular in its horizontal outline. Its dorsal surface has a depression to receive a lateral process of the ethmoid bone.

The maxillaries of all members of the Nannostomina are essentially alike. The maxillary has a single tooth with from one to six cusps. The maxillary is a flat lamella of bone with a robust, conic upper process extending toward the anterior part of the ethmoid. Posteriorly the maxillary does not reach the second infraorbital.

The premaxillary of the Pyrrhulinina bears one to two rows of simple conic teeth while the maxillary has a single row of conic teeth along its edge. The maxillary is elongate and reaches well along the second infraorbital to about the third infraorbital bone. The premaxillaries of members of the Pyrrhulinina is not well divided into upper and lower processes.

The premaxillary in members of the Lebiasinini has a single row of tricuspid teeth similar in general shape to those of the Nannostomina. The premaxillary is fairly well divided into an upper process and a lower lamella. The maxillary has a single row of peglike tricuspid teeth along its anterior edge, and its lower limb reaches to the third orbital bone.

The premaxillary in members of the Erythrininae has well-developed upper and lower limbs and a single row of conical teeth. The maxillary is well developed and in *Hoplias* the fan-shaped distal end is external to the second infraorbital. In *Erythrinus* and *Hoplerythrinus* the fan-shaped distal end of the maxillary is included under the second infraorbital. In the Erythrininae the maxillary almost reaches the third infraorbital.

Lower jaw (figs. 6, 7).—The dentary of adult specimens of the Nannostomina bears two rows of teeth; the anterior large teeth of the outer row have five or six cusps while the posteriormost few teeth may have the number of cusps reduced from one to four. The second row, composed of small conical teeth is on a crest of bone lying behind the replacement teeth of the first row. The shape of the dentary is rather remarkable and diagnostic of the Nannostomina. It is divided into two regions. The anterior region bears the teeth and is approximately like the premaxillary in shape. The posterior portion is of

the more normal characid shape and is of a thinner, lighter bone than the thick anterior region. The two regions are separated by a deep median groove and are joined by a lateroventral connecting sheet of bone. The complicated series of locking bony convolutions present at the symphysis of most characids is absent. The posterior portion of the dentary carries the tube for the laterosensory canal.

The articular lies against the medial posterior surface of the dentary and bears a socket for the articular head of the quadrate. The angular is a well-developed bone ventral and internal to the lower posterior region of the articular and dentary.

The coronomecklian (sesamoidarticular) is a prominent bone on the inside surface of the articular above the posterior region of Meckel's cartilage.

The lower jaw in the Pyrrhulinina is similar in general form and shape to that of *Brycon*. The lower jaw of males of the genus *Copella* is somewhat modified and this is correlated with the differences found in the dentition and shape of the upper jaws (Myers, 1956a, p. 12). There are two rows of conical teeth on the dentary, an outer larger row and an inner row placed on a ridge of bone behind the replacement teeth of the outer row. There is a slight notch along the lower border of the dentary just posterior to the convoluted symphysis. This notch is probably homologous with the deep ventral groove in the dentary of the Nannostomina. The rest of the bones comprising the mandible in the Pyrrhulinina are similar in their basic relationships to those of the Characinae.

In general shape the mandible in members of the Lebiasinini is like that of the Pyrrhulinina; however, the teeth in the outer row are tricuspid and similar in form to those found in the Nannostomina. The inner row is a series of very small conical teeth that, as in the subtribes Nannostomina and Pyrrhulinina, pass onto the lateral upper edge of the jaw behind the first large row of teeth.

The lower jaw in the Erythrininae is not unlike that in the Lebiasinini. In general, the placement of the dentary teeth in these two groups is much alike; however, in the Erythrininae the second row of teeth is restricted to the upper posterior edge of the dentary and to the area posterior to the first row of teeth. This second row does not advance forward on the crest of the bone behind the replacement teeth of the first and largest row of conical teeth.

Mandibular and palatine arches (figs. 4, 6, 7).—Regan (1911, p. 21) stated that *Nannostomus* and *Characidium* belong to the family Hemiodontidae and that these two genera could be distinguished from other hemiodontids by the possession of a single series of teeth in both jaws and a broad two-headed hyomandibular. As shown above, members of the Nannostomina have two rows of teeth in the

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lower jaw. Although examination shows that *Characidium* has a distinctly two-headed hyomandibular, that in the Nannostomina is single-headed. The hyomandibular in the Nannostomina is a broad bone with a broad dorsal articular surface that articulates with both the sphenotic and pterotic. It does not differ greatly in shape or relationships from the hyomandibular in the Characinae. The hyomandibular is not markedly different in shape or functional relationships in Pyrrhulinina, Lebiasinini, or Erythrininae.

The quadrate of *Nannostomus* and *Poecilobrycon* is a large, rather rectangular bone with a long, slender posterior process below the symplectic. The dorsal surface of the quadrate extends upward, lateral to the large mesopterygoid, and the dorsal profile of the quadrate is gently curved. The posterior upper surface contacts the metapterygoid and anterior end of the symplectic through cartilage. The symplectic is quite large, elongate, and rather slab-shaped posteriorly. It is almost as long as the hyomandibular. The metapterygoid posteriorly contacts the lower end of the hyomandibular through cartilage. The central circular fenestra between the quadrate, symplectic, and metapterygoid, so typical of almost all other characids, is absent in the Nannostomina. Just anterior to the upper anterior corner of the quadrate is a small triangular ectopterygoid. In some members of the Nannostomina, this bone bears a few simple conical teeth. In one species, *Poecilobrycon eques*, teeth were found on the ectopterygoid of one side but not the other in some specimens.

The toothless palatine is well developed and lies lateral to the prevomer. The anterior head of the palatine lies just posterior to the upper process of the maxillary.

The mandibular and palatine arches in the Pyrrhulinina and Lebiasinini examined are very similar to those in the Nannostomina, but, in general, these bones are not as elongate as in the Nannostomina. The ectopterygoid is toothless in the Pyrrhulinina but has conical teeth in the Lebiasini, and the bone is always proportionately larger than in the Nannostomina. The fenestra between the quadrate, symplectic, and metapterygoid is absent.

In the Erythrininae, the mandibular and palatine arches are very similar to those of the Characinae. The fenestra between the metapterygoid, quadrate, and symplectic is well developed, and the symplectic is not exceptionally deep at its posterior end. In *Hoplias* the ectopterygoid is a long, thin, tooth-bearing bone extending from the upper part of the quadrate across the inferior surface of the palatine. Anterior to its forward boundary is a small autogenous movable piece of tooth-bearing bone that is connected closely to the ectopterygoid. Sagemehl (1885, p. 95) called this bone the accessory

palatine. For reasons discussed below, I tenatively prefer to call this bone the accessory ectopterygoid. Along the lateral edge of the ectopterygoid and accessory ectopterygoid is a row of large, conical teeth. Medial to this row on both bones is a narrow patch of small, conic teeth. In *Erythrinus* and *Hoplerythrinus* the ectopterygoid extends from the quadrate to over the ventral surface of the palatine (autopalatine). The ectopterygoid in both bears a band of conic teeth. In *Hoplerythrinus*, but not in *Erythrinus*, small conic teeth are present on the ventral surface of the mesopterygoid. In a specimen of *Hoplerythrinus unitaeniatus*, 115 mm. in standard length, from British Guiana, CAS(IUM) 12331, the mesopterygoid teeth are well developed and cover much of that bone's lower surface; however, a specimen from Peru, SU 35044, which is 120 mm. in standard length, has only a few scattered teeth over the mesopterygoid.

Hoedeman (1950b) described a new genus and species in the Erythrininae, *Pseuderythrinus rosapinnis*, from Dutch Guiana. His new genus seems distinguishable from *Hoplerythrinus* only by the number and distribution of teeth on the palatal arch. He recorded a narrow band of teeth on the palatines and no teeth on the "pterygoid" for *Pseuderythrinus*, and he stated that *Hoplerythrinus* has a broad patch of teeth on the palatine and that there are teeth on the pterygoid. Hoedeman's pterygoid is the ectopterygoid of the present account. Examination of a cleared and alizarin-stained specimen and other, nonstained specimens of *Hoplerythrinus* does not confirm Hoedeman's views concerning the placement of teeth in this genus. I find that *Hoplerythrinus* has teeth on the ectopterygoid, no teeth on the palatine, and it may have a broad patch of teeth on the mesopterygoid. The mesopterygoid teeth may be numerous or few and they are usually fewer in small specimens. It seems likely that the specimen, 128 mm. in standard length, forming the basis of Hoedeman's new genus, has as yet failed to develop a dense aggregation of mesopterygoid teeth, and it seems likely that this genus is a synonym of *Hoplerythrinus*. The color and other characters of *Pseuderythrinus rosapinnis* are very much like those of *Hoplerythrinus unitaeniatus;* further investigations probably would indicate that, at most, *P. rosapinnis* is a subspecies of *H. unitaeniatus*. The type of *Pseuderythrinus rosapinnis* needs reexamination.

Hoedeman (1950b, p. 85) recorded palatine teeth present in *Hoplias*, *Hoplerythrinus*, and *Erythrinus* and stated that there are no teeth on the "pterygoid" in *Erythrinus*. This disagrees with what I found in the specimens at hand.

No specimens of these genera were found to have palatine teeth attached to the palatine. This fact is difficult to determine and requires considerable and careful dissection, especially in *Erythrinus*

and *Hoplerythrinus*. In these two genera the tooth-bearing ecopterygoid (= the pterygoid of Hoedeman) is firmly attached to, but not fused with, the palatine. The anterior part of the ectopterygoid lies ventral to the palatine in these two genera and can be mistaken easily for palatine dental plates or dermopalatines. The autogenous tooth-bearing bone below the palatine in *Hoplias* has been described above.

Determination of the homologies of the tooth-bearing elements associated with the autopalatine of the Erythrininae cannot be stated precisely from the examination of adult stages only. The interpretation tentatively adopted here for the morphological situation in *Hoplerythrinus* is based on the following: The ectopterygoid is present and often tooth-bearing in other characids. It is presumed here that the ectopterygoid bone grows anteriorly under the lower surface of the palatines and that the dermal tooth-bearing bones under the autopalatine are not dermopalatine elements that have fused to the ectopterygoid but are simply anterior extensions of the ectopterygoid. The striations and growth pattern of these tooth-bearing bones indicate they are anterior extensions of the ectopterygoid.

The accessory palatine of Sagemehl (1885, p. 95) that occurs in *Hoplias* may be interpreted in two ways, either as a dermopalatine or dental element that has not fused to the ectopterygoid or as an autogenous, anterior piece of the ectopterygoid. Starks (1926, p. 161) maintains that the accessory palatine is homologous with the dermopalatine of *Amia*. This problem cannot be resolved with the information at hand.

Probably the presence of teeth or dental plates associated with the palatine, ectopterygoid, and mesopterygoid is a conservative feature not retained in most other characids; in this respect the tooth pattern of the Erythrininae would be more primitive than that of the other subfamilies of living characids. If this is correct, the separation of the Erythrininae from the rest of the characids might be suspected then to have taken place when the characids had living representatives much more primitive than those extant. In this connection, the morphology and development of the first infraorbital and its relationship to the antorbital in the Erythrininae and possible significance of the infraorbital in the phylogeny of characids and Ostariophysi should be investigated.

Hyoid and branchial arches (fig. 8).—The hyoid arch of *Nannostomus* and *Poecilobrycon* is not unlike that of the Characinae, and the relative positions of the bones of the arches are the same. There are two branchiostegal rays associated with the ceratohyal and one with the epihyal. Members of the tribe Pyrrhulinini also have three branchiostegal rays, while members of the tribe Lebiasinini have four

branchiostegal rays, three associated with the ceratohyal and one with the epihyal. All members of the Erythrininae have five branchiostegal rays, four on the ceratohyal and one on the epihyal.

The branchial arches of the Erythrininae and Lebiasininae are like those of the Characinae and differ mainly in general proportions correlated with different head shape.

Hoedeman (1950a, pp. 17, 19, 25) stated that pharyngeal teeth are absent in three species of his Nannostominae. All specimens of the Nannostomina, however, that I have examined have small, conic pharyngeal teeth much like those illustrated for *Poecilobrycon harrisoni* (fig. 8). The gill rakers of members of the Lebiasininae are simple; however, in the Erythrininae the gill rakers are rather complex. The bony cores of those of the upper limb are truncate with small conical "teeth" along their distal margins while those of the lower limb are serially graduated from truncate ones anteriorly to elongate sharp-pointed laminae of bone posteriorly. The dorsal edges of these laminae bear small conic "teeth" while the anterior truncated gill rakers have "teeth" along their distal borders.

Weberian apparatus (fig. 9).—The Weberian apparatus of the Lebiasininae and Erythrininae is, in all major respects, like that of the genus *Brycon* and the Characinae, differing only in a few aspects of shape and in the proportions of some of the parts. The tripus of *Poecilobrycon harrisoni* is slightly different in shape from that of *Brycon meeki* but still retains the basic characid structure. Its dorsal proximal portion is placed slightly higher and more anterior on the body of the third vertebra. In some specimens of the Nannostomina examined there are small contingencies of bone across the joint between the neural pedicel and the neural complex.

Pectoral girdle (fig. 10).—The pectoral girdle of *Poecilobrycon harrisoni* is much like that of the Characinae, having a large medial coracoid lamina. The main body of the cleithrum, like that of the Characinae, is a sickle-shaped lamella; however, the large foramen between the coracoid and the cleithrum, so typical of the Characinae, is absent or at best only a slight opening. The supracleithrum lacks a sensory canal in all members of the Nannostomina and the post-temporal is not forked, the lower spinous process found in the Characinae being absent. The relationships of the postcleithrum, mesocoracoid, and scapula are not markedly different from those of the Characinae.

In the Pyrrhulinina, sensory canals are lacking in the post-temporal and supracleithrum, and the post-temporal is not forked. The rest of the pectoral girdle is typical of that of characids. Unlike the Nannostomina, the Pyrrhulinina have a large foramen between the coracoid and the cleithrum. In speicmens of *Lebiasina* and *Pia-*

bucina, the foramen between the coracoid and cleithrum is well developed. The rest of the pectoral skeleton in these two genera is like that of the Characinae.

The pectoral girdle of the Erythrininae is unique among characids. The lower limb of the cleithrum is long and slender. The lateral inferior lamella is much reduced in extent. The median coracoid lamella is extremely reduced in size, being a very narrow crest or actually absent. In all other characids that I have examined, the coracoid extends anteriorly to, or almost to, the anterior edge of the cleithrum. In the Erythrininae, the coracoid extends anteriorly for only about one-half the length of the lower limb of the cleithrum, and the foramen between the cleithrum and coracoid is absent. The cleithrum and post-temporal of the Erythrininae contain segments of the laterosensory canals.

Classification of the Characid Subfamilies Lebiasininae and Erythrininae

The following classification is based primarily on the evidence presented in the foregoing section.

SUBFAMILY LEBIASININAE EIGENMANN, 1910

Definition: (1) Large fenestra between quadrate and metapterygoid absent. (2) Two diverging lamellae on ventral surface of ethmoid very poorly developed. (3) Lateral posterior edge of frontal not articulated with spinous process of sphenotic. (4) Six infraorbital bones present; antorbital and first infraorbital separate ossifications. (5) Accessory ectopterygoid (or dermopalatine?) absent. (6) Lower limb of cleithrum moderately stout, not long and slender, its lateral inferior lamella large. (7) Coracoid lamella a large flat plate, reaching to near anterior border of cleithrum. (8) Anastomosis between supraorbital and dermopterotic canal present. (9) Parietal and epiphyseal branches of supraorbital canal reduced in length, parietal branch never reaching parietal bone. (10) Perforated lateral line scales, when present, confined to region anterior to dorsal fin. (11) Frontal fontanel always absent in adults. (12) Teeth well developed in both jaws, unicuspid or multicuspid. (13) Premaxillary with one tooth row. (14) Dentary usually with two rows of teeth. (15) Gape short, not reaching orbit, or, at most, only reaching posteriorly little beyond verticle with anterior margin of orbit. (16) Branchiostegal rays three or four. (17) Gill membranes partially united but free from isthmus. (18) Body elongate, often fusiform or with fairly blunt head; body rounded in cross section in region of dorsal fin and head, compressed in region of caudal peduncle. (19) Adipose fin

present or absent. (20) Anal fin short-based, with 8 to 14 rays. Males often with specialized anal fin rays; these expanded in anterior-posterior plane and often thickened laterally. (21) Dorsal fin always in advance of anal fin, placed over pelvic fins. (22) Caudal fin rounded or forked. (23) Scales large, 6 to 7 horizontal rows between dorsal and pelvic fines, 18 to 30 scales in longitudinal series.

The tribes of subfamily Lebiasininae are:

Lebiasinini Eigenmann, 1910
Pyrrhulinini Eigenmann, 1910

TRIBE LEBIASININI EIGENMANN, 1910

Nomenclatural note: Eigenmann (1910) was the first to base a family group name, Lebiasininae, on the genus *Lebiasina*. Hoedeman (1950b) was the first to propose the use of this family group name as a tribe.

Definition: (1) Four branchiostegal rays. (2) Premaxillary divided into well-developed upper and lower rami. (3) Premaxillary teeth tricuspid, in one row. (4) Dentary with teeth in two rows, outer row teeth tricuspid, inner with simple, conic teeth. (5) Dentary without inferior deep notch or groove, ventral surface smooth. (6) Parietal branch of supraorbital sensory canal moderately well developed, reaching almost to parietal bone. (7) Supratemporal laterosensory canals present. (8) Dermopterotic laterosensory canals present. (9) Extrascapular laterosensory canals and bones present. (10) Supracleithrum with laterosensory canal. (11) Frontalpterotic joint present on surface of skull.

The genera of tribe Lebiasinini are:

Lebiasina Valenciennes (1846), with two species.
Piabucina Valenciennes (1849), with six or seven species.

Remarks: *Lebiasina* has been separated from *Piabucina* by the absence of an adipose fin in the former and its presence in the latter. This is apparently a poor character in these fishes, for, as Eigenmann (1923, p. 123) noted, some specimens of *Lebiasina bimaculata* and *Lebiasina multimaculata* occasionally have an adipose fin. In the specimens I have been able to examine, the anterior wall of the posterior division of the swimbladder in *Lebiasina bimaculata* and *Piabucina festae* is "cellular" while in *Piabucina erythrinoides* and *Piabucina panamensis* it is not. The tribe Lebiasinini needs revision at the specific and generic level.

TRIBE PYRRHULININI EIGENMANN, 1910

Nomenclatural note: Eigenmann (1910) was the first to base a family group name, Pyrrhulininae, on the genus *Pyrrhulina*. Hoedeman (1954a) was the first to propose the use of this family group name as a tribe Pyrrhulinini.

Definition: (1) Three branchiostegal rays. (2) Premaxillary only weakly, or not at all, divided into upper and lower processes. (3) Premaxillary teeth simple conic to hexacuspid, in one or two rows. (4) Dentary with teeth in two rows, uni- to hexacuspid. (5) Dentary with inferior notch below or deep groove continuous with foramen for mental ramus of mandibular branch of trigeminal nerve. (6) Parietal and epiphyseal branches of supraorbital laterosensory canal extremely short, usually not over one or, rarely, two millimeters long even in largest specimens of largest species; parietal canal not reaching parietal bone. (7) Supratemporal laterosensory canal absent. (8) Dermopterotic canal absent. (9) Extrascapular laterosensory canals and bones absent. (10) Supracleithrum without enclosed laterosensory canal. (11) Frontal-pterotic joint absent, pterotic being excluded from contact with frontal by sphenotic.

The subtribes of tribe Pyrrhulinini are:

Pyrrhulinina
Nannostomina

SUBTRIBE PYRRHULININA EIGENMANN, 1910

Definition: (1) Premaxillary-ethmoid articulation a very slightly movable, syndesmotic (fibrous) joint. (2) In adults, posterior shaft of prevomer reaches parasphenoid. (3) Preopercle extends anteriorly to near articular. (4) Maxillary bone extends posteriorly to region of second orbital. (5) Premaxillary with unicuspid teeth. (6) Teeth of dentary unicuspid, in two rows. (7) Dentary not divided into two well-defined regions by a deep ventral groove continuous with mental foramen. Dentary with notch below region of mental foramen. (8) Inferior portion of post-temporal fossa extremely large, its anterolateral border extending anterior to, or beyond, synchondral portion of joint between sphenotic and pterotic bones, anteriorly beyond vertical from anterior edge of auditory foramen.

The genera of subtribe Pyrrhulinina are:

Pyrrhulina Valenciennes (1846), with perhaps a dozen species
Copeina Fowler (1906), with two or three species
Copella Myers (1956a), with four or five species

SUBTRIBE NANNOSTOMINA EIGENMANN, 1909

Nomenclatural note: Eigenmann (1909a) was the first to base a family group name, Nannostomatinae, on the genus *Nannostomus*. The proper spelling of this family group name should have been Nannostominae (Miller, 1897, p. 132).

Definition: (1) Premaxillary-ethmoid articulation a loose movable syndesmotic (fibrous) joint connected by fairly long, interosseous ligaments, but premaxillary not protractile, synovial joint absent.

(2) Posterior shaft of prevomer reduced or absent in adults and young, never reaching parasphenoid. (3) Preopercle not reaching near articular, extending anteriorly only to lower posterior process of quadrate. (4) Maxillary confined to anterior region of first infraorbital bone. (5) Premaxillary teeth 1- to 6-cusped, usually 3- to 6-cusped, multicuspid teeth flattened and incisor-like. (6) Dentary with outer row of flattened, 3- to 6-cusped incisor-like teeth and one inner row of unicuspid conic teeth. (7) Dentary divided into two distinct regions by a deep inferior groove continuous with the mental foramen. (8) Lower portion of post-temporal fossa not enlarged, its anterolateral border well posterior to vertical from synchondral joint between sphenotic and pterotic, anterolateral border of post-temporal fossa behind vertical from anterior edge of auditory foramen.

The genera of subtribe nannostomina are:

Nannostomus Günther (1872), with five or six valid species
Poecilobrycon Eigenmann (1909b), with three valid species

Note that *Nannobrycon* of Hoedeman (1950a) is here considered a subgenus of *Poecilobrycon* and *Archicheir* Eigenmann (1909b) is considered a synonym of *Poecilobrycon*. *Archicheir minutus* Eigenmann (1909b), the type of *Archicheir*, is based on the young of *Poecilobrycon harrisoni* Eigenmann (1909b). A review of the genera and species of the Nannostomina is in preparation.

SUBFAMILY ERYTHRININAE GILL, 1858

Definition: (1) Large fenestra between quadrate and metapterygoid present. (2) Two diverging lamellae on ventral surface of ethmoid well developed. (3) Lateral posterior edge of frontal articulated with spinous process of sphenotic. (4) Six infraorbital bones present; first infraorbital apparently fused with antorbital. (5) Accessory ectopterygoid (or dermopalatine) present, ventral to autopalatine either as an autogenous element or fused with ectopterygoid. (6) Lower limb of cleithrum long and slender, its lateral inferior lamella small. (7) Coracoid lamella small or absent, not large, flat plate as in other characids, not reaching to near anterior border of cleithrum. (8) Anastomosis between supraorbital and dermopterotic laterosensory canal absent. (9) Parietal and epiphyseal branches of supraorbital canals well developed, parietal canal reaching parietal bone. (10) Perforated lateral line scales present, continued uninterrupted to caudal fin. (11) Frontal fontanel always absent in adults. (12) Teeth well developed, unicuspid, conic in both jaws. (13) Premaxillary with one tooth row. (14) Dentary with anterior tooth row bordering length of jaw, inner tooth row confined to posterior portion of mandibular ramus. (15) Gape long, reaching

posteriorly beyond vertical from anterior border of orbit. (16) Branchiostegal rays five. (17) Gill membranes partially united but free from isthmus. (18) Body elongate, with blunt head and snout; body rounded in cross section in region of dorsal fin and head, compressed in region of caudal peduncle. (19) Adipose fin absent. (20) Anal fin short-based, with about 10 to 12 rays. (21) Dorsal fin always in advance of anal fin, usually over pelvic fins. (22) Caudal fin rounded in profile. (23) Scales moderate to fairly large, about 30 to 45 in a lateral series, about 7 to 12 in horizontal rows between dorsal and pelvic fins.

The genera of subfamily Erythrininae are:

Hoplias Gill (1903), with one or two species
Erythrinus Scopoli (1771), with one species
Hoplerythrinus Gill (1895), with one species
Pseuderythrinus Hoedeman (1950b), with one species, status uncertain

Remarks: Of the characters listed above, 3–8 seem to be diagnostic for the subfamily, distinguishing its members from all other characids.

Relationships of the Subtribe Nannostomina and its Close Relatives, the Pyrrhulinina

The classification above clearly indicates the close relationship of the Nannostomina and Pyrrhulinina. The unique structure of the dentary in these two groups, together with the accumulation of such characters as three branchiostegal rays, a premaxillary without a clear upper or lower process, short parietal and epiphyseal laterosensory canals, no supratemporal or dermopterotic canals, no extrascapular bone or canal, no canal embedded in the supracleithrum, and the lack of a frontal-pterotic joint, cannot be due to convergent evolution but only to a common ancestry. Further inspection of these fishes reveals other similarities; for example, their scales are almost identical in shape and structure, both groups have members with modified anal fin rays in the males, both have a tendency to lose canals in orbital bones, and one species, *Nannostomus espei*, has a color pattern remarkably like that of *Pyrrhulina vittata* and *Pyrrhulina spilota*. *Nannostomus espei* also has scales that more closely approach the shape of those of *Pyrrhulina* than the scales of any other species in the Nannostomina. The osteology of *Nannostomus espei*, however, is typically that of *Nannostomus*.

The Nannostomina are specialized for feeding on small animal organisms that occur on plants, rocks, and other objects. They also feed on slowly moving free-living organisms. Their movements are relatively slow and precise. The Pyrrhulinina are more active and more predaceous, having larger mouths, attacking larger prey, and

striking their prey harder. The jaws of the Nannostomina are far more specialized than those of the Pyrrhulinina. The large post-temporal fossa in the Pyrrhulinina is an interesting specialization. The large amount of muscle tissue found in this area undoubtedly is associated functionally with feeding and swimming behavior, but this needs further study.

In addition to the differences between the Pyrrhulinina and Nannostomina noted in the classification above, these two groups have a consistent difference in body shape. The body form in the Nannostomina usually is smoothly fusiform, whereas that in the Pyrrhulinina is not, the profile showing a slight notch behind the dorsal fin, the belly being more or less flat, and the back being less arched. Of all the species in the Nannostomina, *Nannostomus espei* has a body shape closest to that of the Pyrrhulinina.

Despite the differences between the Pyrrhulinina and the Nannostomina, I believe they may be united justifiably in the tribe Pyrrhulinini, based on the morphological characters listed above.

The relationships of the Pyrrhulinini are, without doubt, with the Lebiasinini, and these two tribes form the subfamily Lebiasininae. The characters listed in the classification for this subfamily (p. 148) are held in combination by no other characids. A full discussion of the relationships between the Lebiasinini and the Pyrrhulinini should await fuller treatment of the genera in these two tribes.

From the information at hand it seems safe to conclude that the Pyrrhulinini were derived from characids somewhat similar perhaps to the existing members of the Lebiasinini and that the Pyrrhulinina and the Nannostomina had a common ancestor. Neither of these two subtribes can be derived from the other, but their common ancestor must have differed from the recent members of the Lebiasinini in the structure of the jaws and reduction of the laterosensory system of the head.

Relationships of the Lebiasininae and Erythrininae

What are the relationships of the Lebiasininae and Erythrininae that can be determined from the present osteological study? Considering the absolute lack of fossil evidence in this case, inferences about phylogenetic relationships based on recent material are bound to bear only a vague resemblance to the actual course of evolution; nevertheless, an attempt should be made to indicate relationships even if this involves nothing more than noting that certain groups appear associated because they have a certain number of characters in common.

The relationships of the Erythrininae to other recent characids remain rather obscure. They are not close to the Characinae and they do not appear derived from them. A consideration of the primitive versus specialized aspects of their skeleton may give some hint regarding their relationships. In general, a reduction in number of branchiostegal rays in teleosts can be considered a specialized feature (Hubbs, 1919). In all probability, the presence of five branchiostegal rays in the Erythrininae is relatively primitive for characids. The absence of the supraorbital in both the Erythrininae and the Lebiasininae probably is specialized and I suspect that this is also true for the morphology of the antorbital in the Erythrininae. Dental plates and teeth associated with the palatine, ectopterygoid, and mesopterygoid in the Erythrininae is probably a primitive feature in these fishes. The unique absence of a connection between the dermopterotic and supraorbital laterosensory canals in the Erythrininae probably is specialized. Whether the articulation between the sphenotic and frontal in the Erythrininae is primitive or specialized cannot be said. It would seem that the pectoral girdle of the Erythrininae is rather specialized because the interosseus space, usually present in teleosts and other subfamilies of characids (Starks, 1930, p. 90), is absent; however, the gross morphology of the pectoral girdle of the Erythrininae is in some respects similar to that of *Amia* and it is possible that the form of the pectoral girdle in the Erythrininae is rather primitive. Likewise, it is difficult to evaluate the generalized (versus specialized) nature of other characters of the Erythrininae. The short-based anal fin is probably primitive with regard to the Characidae and Cypriniformes as a whole, and the same may be true of the large scales. It is also possible that the rather blunt, cylindrical body shape is primitive.

Examination of the osteology of *Hepsetus* indicates certain relationships with *Erythrinus* and *Hoplias*. Bertmar (1959, p. 350; and in litt.) has noted that *Hepsetus* is more primitive from the embryological point of view than the other ten characids he examined and that all the characids he investigated are more primitive in certain respects than *Amia*. This of course does not mean that characids are more primitive than *Amia*, but it does pose questions about the origins of the Cypriniformes. The Erythrininae appear to be more primitive osteologically than *Hepsetus*. Investigation of the ontogeny of their chondrocranium should be very fruitful.

About all that can be concluded here is: (1) the Erythrininae are definitely characid in morphology; (2) but their basic structure is more remote from that of the so-called "central group of characids" (i.e., the Characinae) than of any other known living characid; (3) they probably were not derived from a characid ancestor that was

like any living member or members of the Characinae. There is perhaps more reason to give separate family status to the Erythrininae than to any other subfamily of characids. Also there is some reason to suspect that at least in certain features, the Erythrininae are the most archaic of living characids. In other aspects, however, they are possibly quite specialized.

What are the relationships of the subfamily Lebiasininae? Superficially, members of the tribe Lebiasinini look much like members of the Erythrininae because of their large scales, short-based anal fin, and the overall similar appearance of the body and head. In addition, both groups lack the supraorbital. The last is possibly not too important a character, for loss of an element probably never should be considered as important as the development of a new structure. Except for the fact, however, that these two groups are characids and have similarly shaped cranial bones because of their similar general body and head shape, they have little in common osteologically. In all the unique respects in which the Erythrininae differ from the Characinae, the Lebiasininae are like the Characinae. As noted above, members of the tribe Lebiasinini and indeed the entire Labiasininae have a few very unique characters that are different from those of both the Characinae and the Erythrininae. The unique lack of a fenestra between the quadrate and metapterygoid appears specialized. Also, the general reduction in the laterosensory canals of the head of the Lebiasininae and the unique laterosensory head canals of the member subtribes of the Pyrrhulinini are very specialized. It seems likely (1) that the Lebiasininae are somewhat more closely related to the Characinae than to the Erythrininae and (2) that the Lebiasininae evolved from a common characid stock that gave rise to Lebiasininae and Characinae but not to the Erythrininae.

According to several authors, one of the distinguishing characters of the Lebiasinini is the possession of a "cellular" anterior wall of the posterior chamber of the swimbladder. The present investigation indicates that certain species (*Piabucina panamensis* and *P. erythrinoides*) in this group lack this feature while others (*Lebiasinina bimaculata* and *Piabucina festae*) do have it. Obviously, the group needs revision and, since Böhlke (1958, p. 94) has indicated he is doing this, no revision is attempted here. It should also be noted that, of the Erythrininae, at least *Hoplerythrinus unitaeniatus* and *Erythrinus erythrinus* have a cellular anterior wall of the posterior chamber of the swimbladder. *Hoplias malabaricus* does not. The significance of the similar "cellular" structure of swimbladders of some members of the Erythrininae to that of some of the Lebiasinini is difficult to assess. In view of the distinct osteological differences between the Erythrininae and the Lebiasinini, however, I prefer to believe that

this equivalence of structure is due to similar adaptation to stagnant water and that it does not indicate close genetic relationships. Osteological comparisons indicate that the Lebiasininae are not related closely to such genera as *Anostomus*, *Leparinus*, and *Hemiodus*.

Summary

The primary results of this study are as follows: The Lebiasininae and Erythrininae are defined and their relationships to each other and to other characids are discussed. The Lebiasininae are not related closely to the Erythrininae as assumed by many earlier authors. The Erythrininae cannot have been derived directly from ancestors that were like recent members of the Characinae (as defined by Weitzman, 1962, p. 48). Although the evidence is inconclusive, of all living characids, the Erythrininae are probably the most conservative (in some ways). It is surmised that the Characinae and Erythrininae were derived from a common characid stock remote in time and morphology from these two subfamilies as they are known today. The Lebiasininae, in many important respects, are more closely allied morphologically to the Characinae than to the Erythrininae despite their superficial resemblance to the Erythrininae. It appears that the Lebiasininae may have been derived from early members of the Characinae or at least from ancestral characids that were more like the Characinae than the Erythrininae in their morphology.

The subfamily Lebiasininae consists of two tribes, the Lebiasinini and the Pyrrhulinini. Both are defined herein. The Lebiasinini needs revision, but no attempt was made to reevaluate in this study its genera and species. The Pyrrhulini consists of two subtribes, the Pyrrhulinina and the Nannostomina, and both are defined herein.

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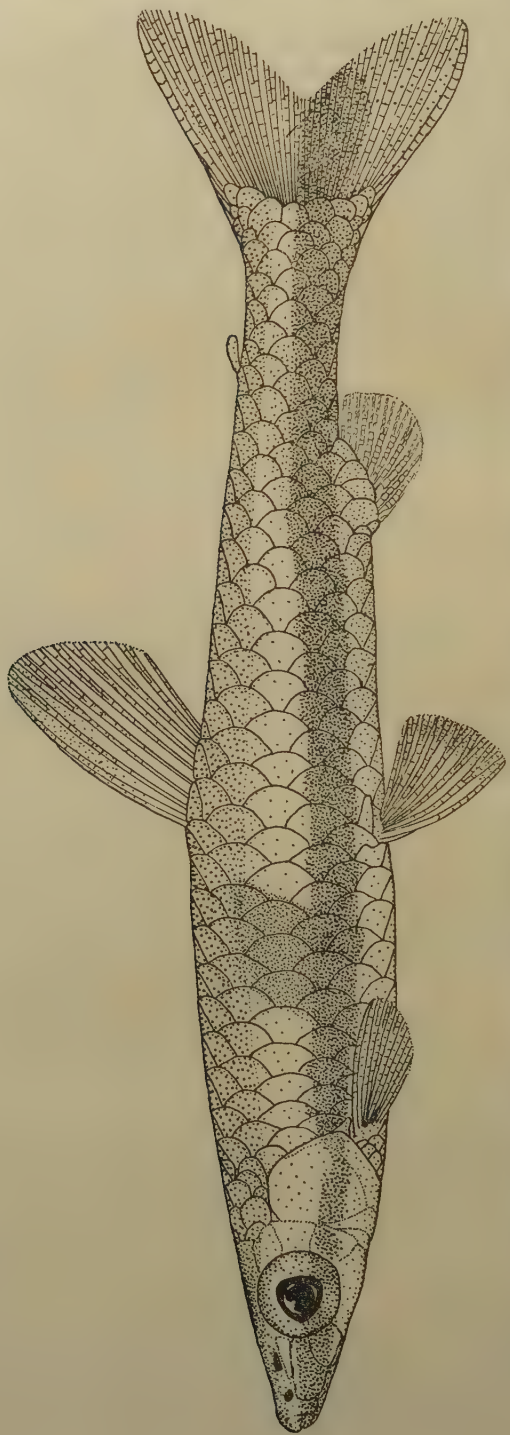

FIGURE 1.—Lateral view of a male *Poecilobrycon harrisoni* Eigenmann, SU 50243, 38.5 mm. in standard length. Georgetown, British Guiana.

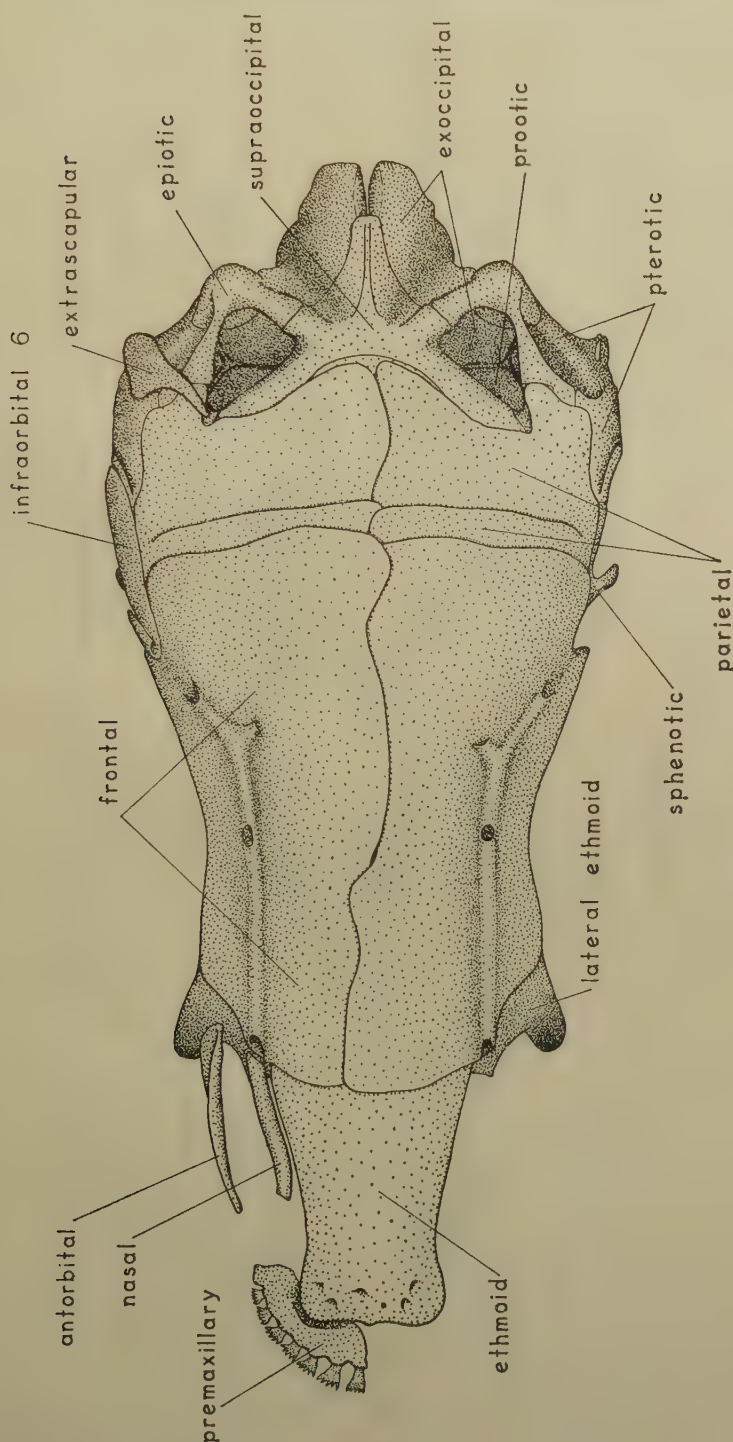

FIGURE 2.—Cranium of *Poecilobrycon harrisoni* (dorsal view).

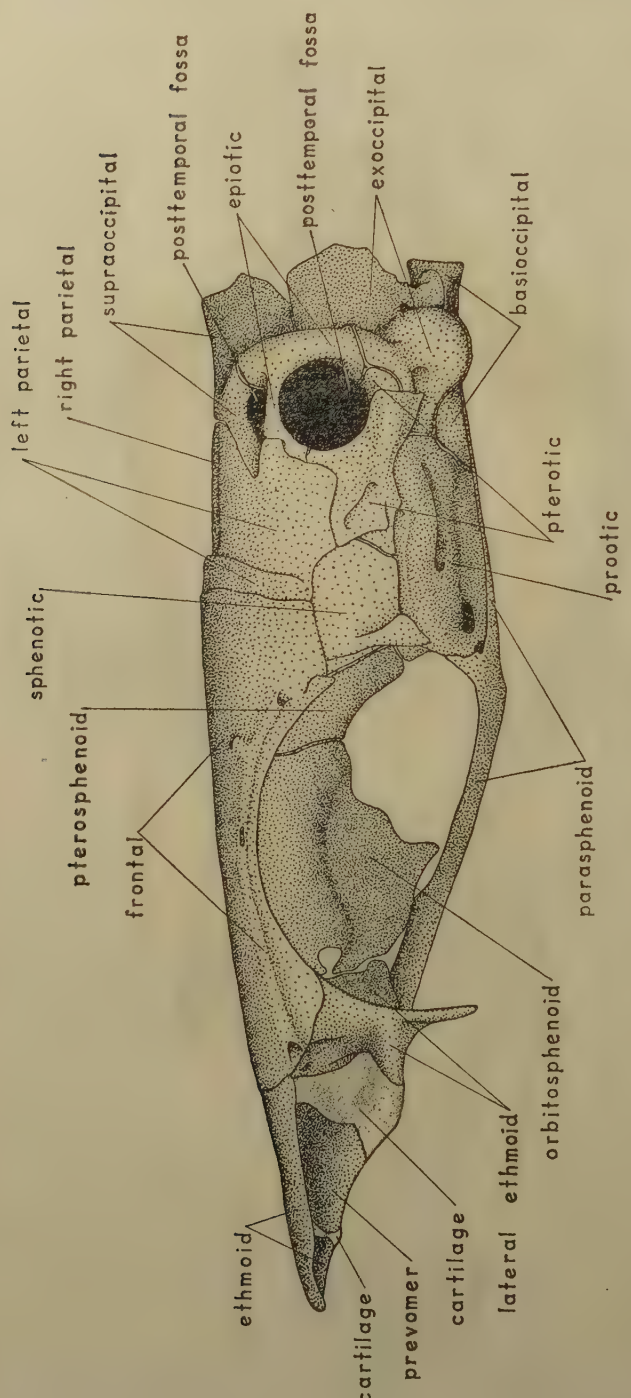

FIGURE 3.—Cranium of *Poeciliobrycon harrisoni* (lateral view).

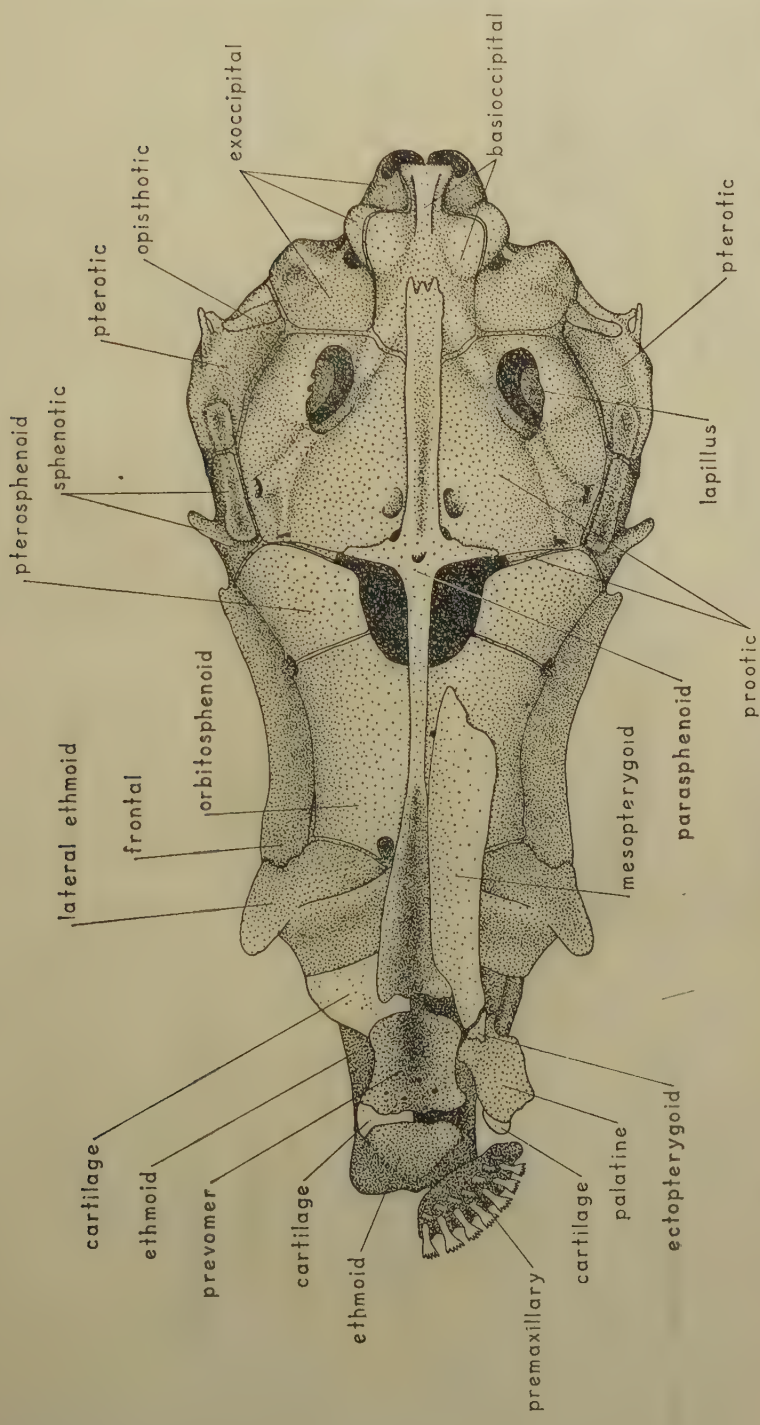

FIGURE 4.—Cranium of *Poecilobrycon harrisoni;* also illustrated are the right premaxillary and the right platine arch (ventral view). The cartilage between the ethmoid, prevomer, and lateral ethmoid is shown on the left side only.

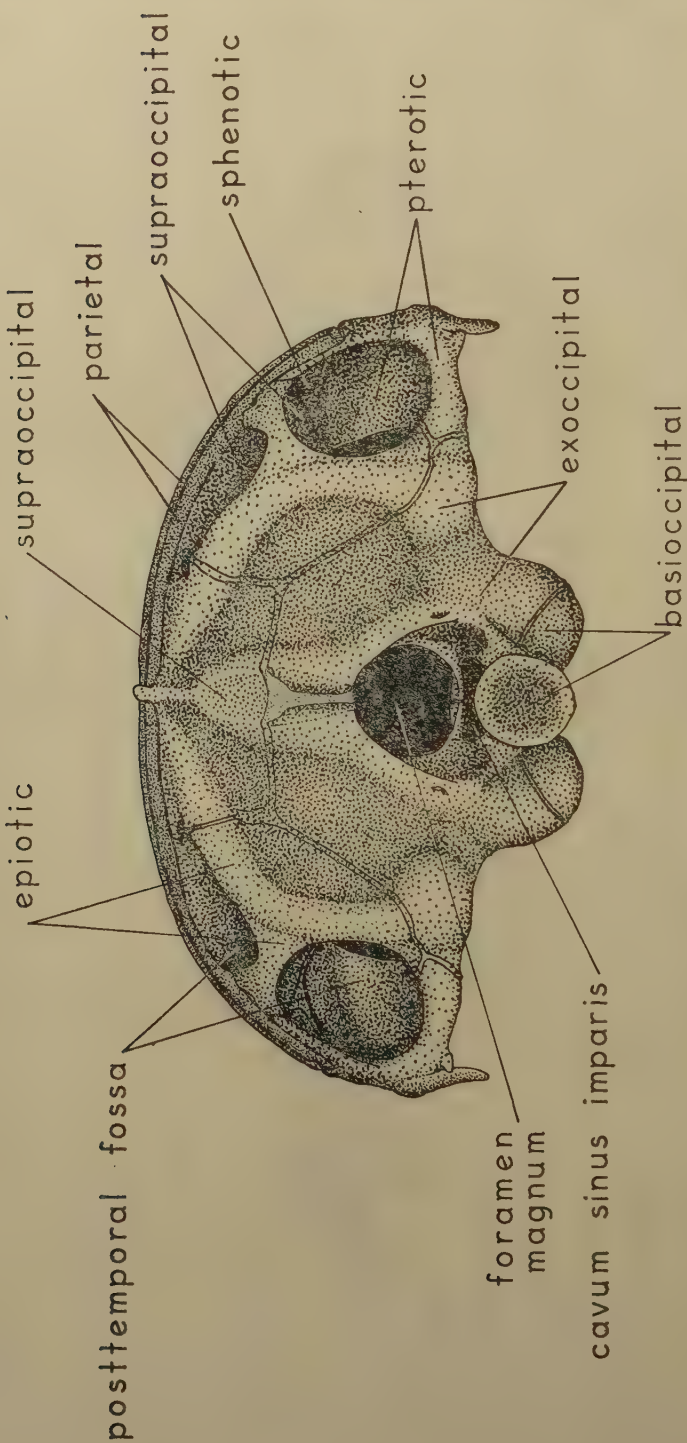

FIGURE 5.—Cranium of *Poecilobrycon harrisoni* (posterior view).

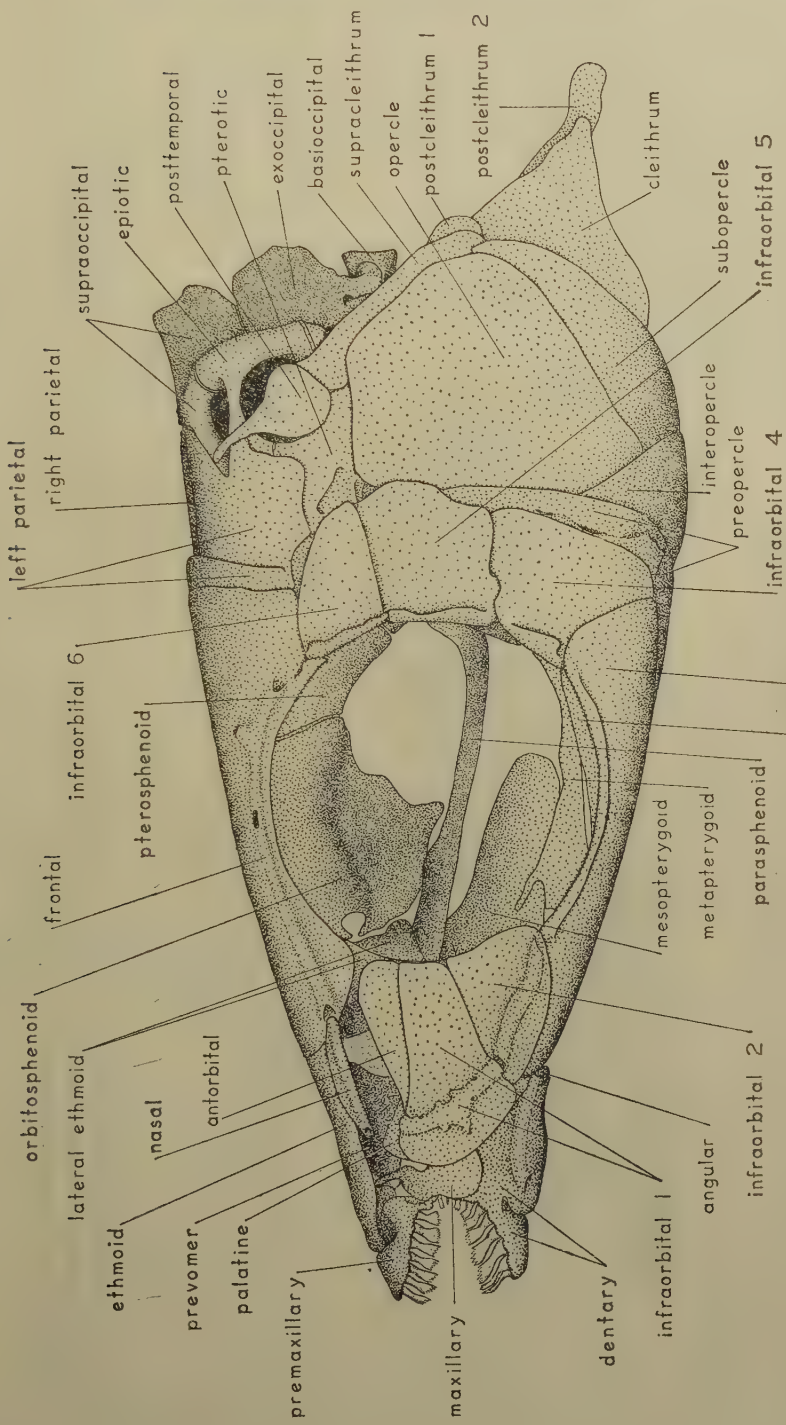

FIGURE 6.—Skull of *Poecilobrycon harrisoni*, including part of the pectoral girdle (lateral view).

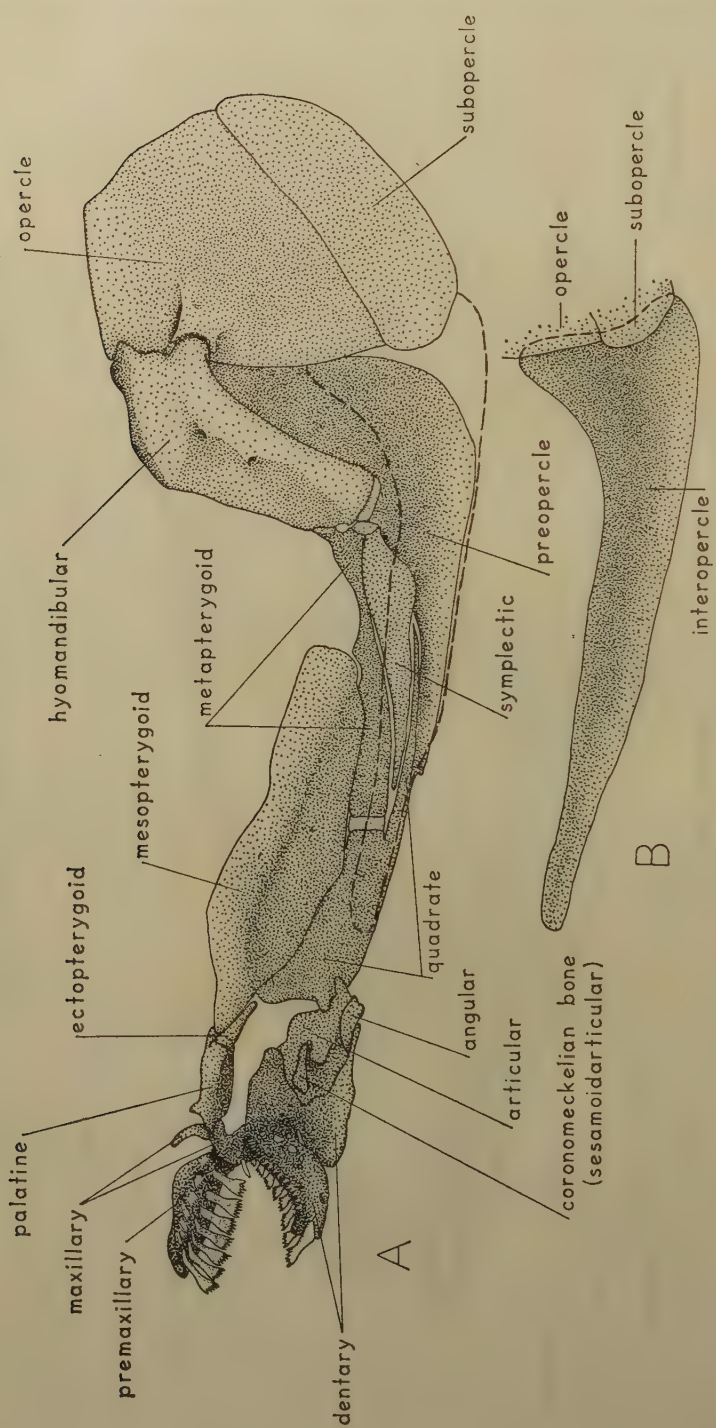

FIGURE 7.—Lateral bones of the face of *Poecilobrycon harrisoni* (median view): A, The lateral facial bones are shown with the interopercle removed but its position shown by the broken lines. B, The interopercle, showing its relation to the opercle. The posterior border of the interopercle is lateral to the opercle and the subopercle and is shown by a broken line.

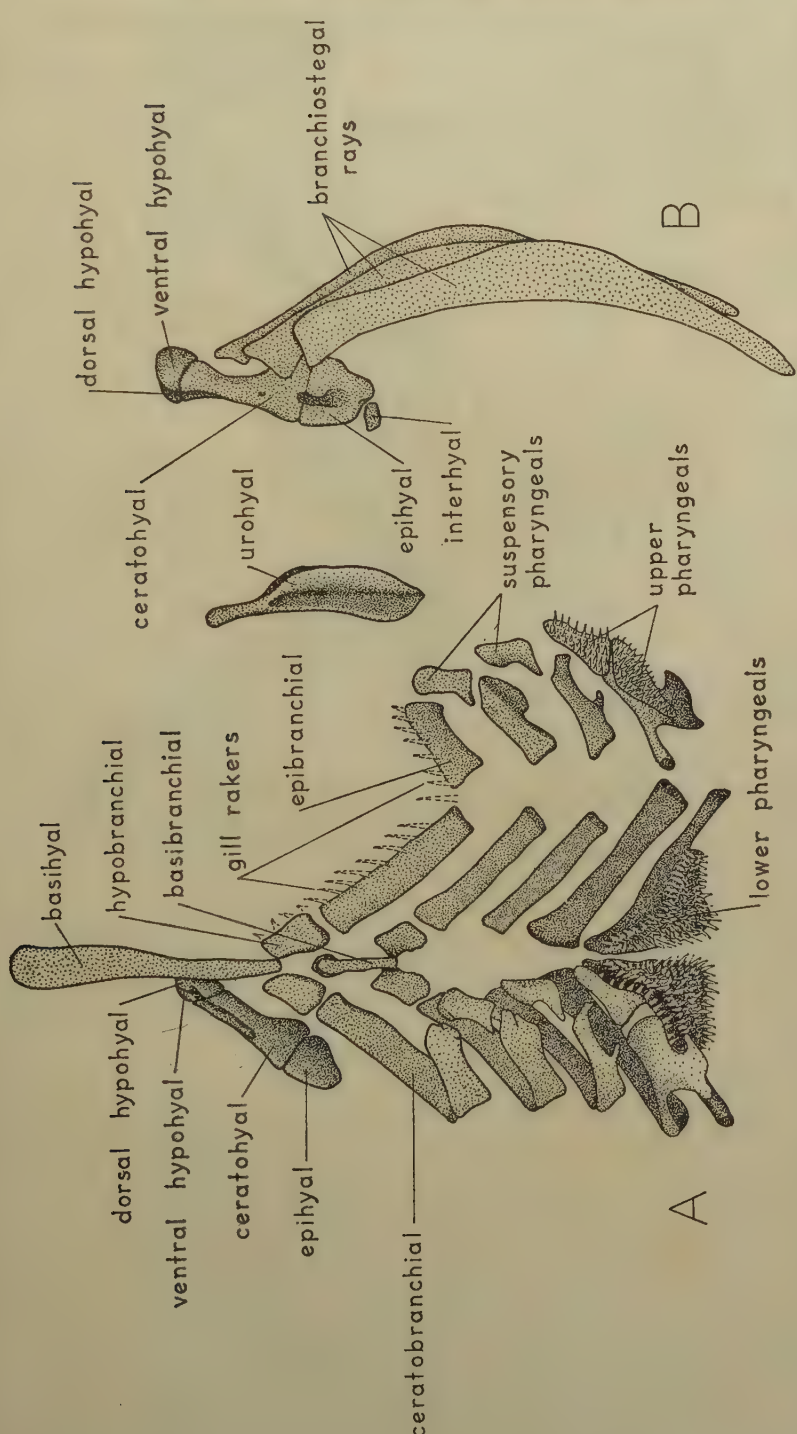

FIGURE 8.—Hyobranchial apparatus of *Poecilobrycon harrisoni*: A, Hyoid arch (left side), branchial arches, and urohyal. Branchial arches and hyoid arch in dorsal view except upper element of right side in ventral view. Urohyal in right lateral view. B, Hyoid arch and branchiostegals (right side, lateral view).

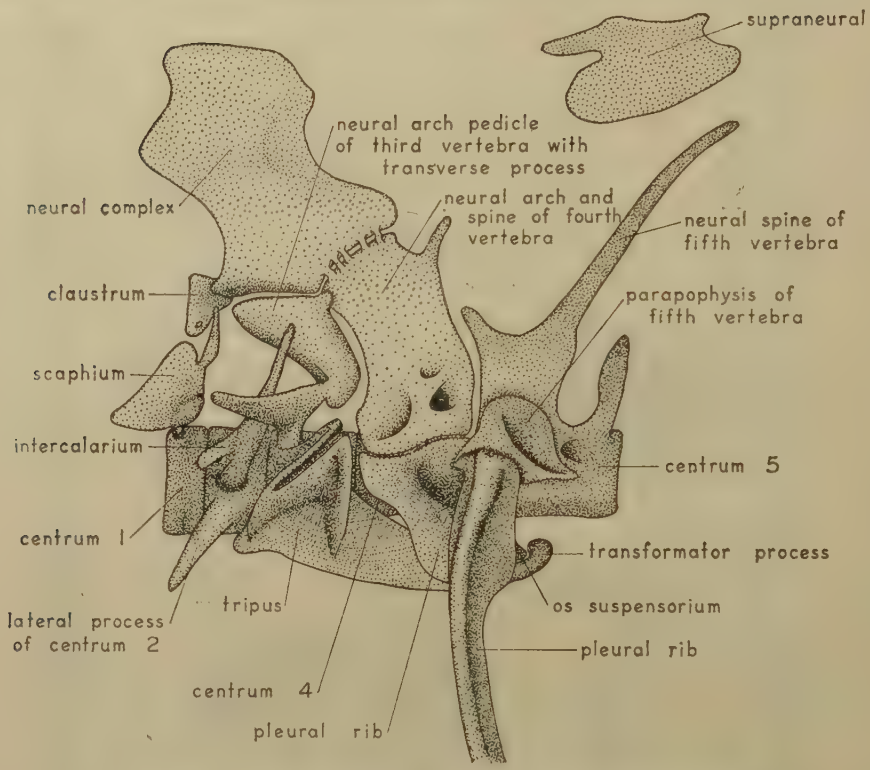

FIGURE 9.—Weberian apparatus of *Poecilobrycon harrisoni* (lateral view).

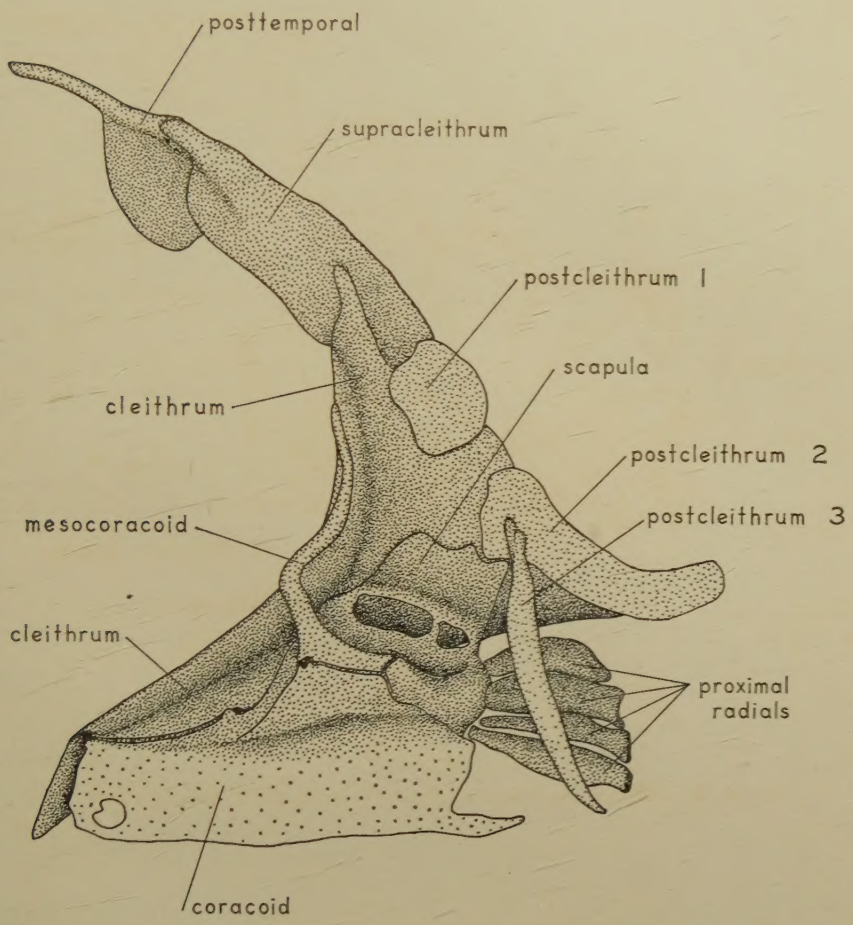

FIGURE 10.—Right pectoral girdle of *Poecilobrycon harrisoni* (median view). The fin rays have been removed.

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